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CHATTY FEMALES AND QUIET MALES: COMPLEX VOCAL COMMUNICATION IN THE NORTHERN DTELLA, *GEHYRA DUBIA*

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***Abstract.*—Vocal communication is widely used by vertebrates to transfer complex information to conspecifics. Although most birds, mammals, frogs, and crocodilians communicate vocally, most squamate reptiles are mute and unable to broadcast sound signals. Notable exceptions are gekkonid lizards, in which vocal communication is phylogenetically widespread. We describe the vocal repertoire of a house gecko native to tropical Australia, the Northern Dtella (*Gehyra dubia*). Male and female *Gehyra dubia* vocalize at a high frequency range (from 6,000–13,000 Hz, almost above the limits of human hearing), and produce at least five different vocalizations. Both sexes produce single chirp calls more often than more complex call types, suggesting that these serve as broadcast signals. More complex vocalizations (multiple single chirps, multiple double chirps, and triple chirps) are frequently used in the presence of another individual. Multiple single chirp calls appear to be used exclusively by males, whereas the other four calls are made by both sexes. Female geckos vocalized significantly more often than males, both when alone and when paired with a conspecific, especially a male. The calling rates of paired geckos are strongly correlated, suggesting active vocal communication between individuals. The vocal repertoire of *G. dubia* is among the most complex yet studied among squamate reptiles, and individuals modify calling rates according to sex, body size, and social context. Such complexity in vocal communication may help nocturnal geckos efficiently establish and maintain territories, find mates, and avoid direct conflicts with conspecifics.**

Key Words.—calling behavior; communication; signaling; sound production; vocal communication; vocalization

INTRODUCTION

Most vertebrates communicate with conspecifics and sometimes with other species, although the channels of communication vary substantially among taxa (Bradbury and Vehrencamp 1998). Vocalizations are a major mechanism of information transfer in many vertebrate groups, and can be used to indicate the presence of food (Hauser and Marler 1993), to demarcate territorial boundaries, attract mates, and communicate the presence of predators (Jono and Inui 2012). Vocal communication has been studied extensively in mammals, birds, and frogs because most species in these groups produce distinctive vocalizations audible to a wide range of animals, including humans (Bradbury and Vehrencamp 1998). Despite vocal communication in reptiles being phylogenetically widespread, we know comparatively little about vocal communication in this diverse group.

The best known reptile vocalizations are in the Crocodilia (crocodiles, alligators, and their relatives). Adult crocodiles use vocal communication during courtship and territory defense (Garrick and Lang 1977). Juvenile crocodiles vocalize to signal to their mother while still in the egg, to stimulate her to open the nest (Vergne et al. 2009), to signal the mother to provide protection when offspring are threatened (e.g., distress calls), and between siblings to maintain social coherence among nest mates (Vergne et al. 2007, 2011, 2012). In squamate reptiles (snakes and lizards), vocalizations are generally restricted to lizards, including anguids, gekkonids, helodermatids, varanids, and a few iguanian lizards (Gans 1969), although at least one snake species has vocal cords and emits at least two types of defensive sounds (*Pituophis melanoleucus*; Young et al. 1995). Other lizard species sometimes "squeak," but only when captured or attempting to bite (Carothers et al. 2001). Geckos are unique among lizards in possessing vocal cords that facilitate the production of complex vocalizations (Marcellini 1977; Moore et al. 1991; Tang et al. 2001). Vocalizations are phylogenetically and geographically widespread in gekkonid lizards; of the ~2,000 species of geckos worldwide, species in at least 20 genera produce sounds (Table 1; Bauer et al. 1992).

Vocalizations can vary in pitch, intensity, frequency, and temporal pattern, and can be aimed at very specific receivers or broadcast widely (Marcellini 1977). Gecko vocalizations are typically relatively short in duration, comprised of a single burst of sound with a dominant frequency ranging from 1,000 Hz (e.g., the genus *Eublepharis*) to 4,000 Hz (e.g., *Gekko gecko*; Sams-Dodd and Capranica 1996). Generally, both males and females of a single species can vocalize and calls can be audible from less than a few meters to over 20 m away (Tang et al. 2001). Although some studies report that only male geckos vocalize during aggressive encounters

TABLE 1. Review of the gecko genera in which vocal communication has been studied.

Family	Genus	Reference
Gekkonidae	*Calodactylodes*	Werner et al. 2008
	Gekko	Marcellini 1977; Wever et al. 1966; Tang et al. 2001; Jono and Inui 2012
	Gehyra	Tremul 2003
	Hemidactylus	Marcellini 1974, 1977; Frankenberg 1982
	Homopholis	Schäfer 1994 (in Russell et al. 2000)
	Lygodactylus	Kastle 1964 (in Marcellini 1977)
	Pachydactylus	Loveridge 1947
	Phelsuma	Kastle 1964 (in Marcellini 1977)
	Ptenopus	Haacke 1969; Hibbitts et al. 2007
	Uroplatus	Henkel and Schmidt 1991; Glaw and Vences 1992 (in Russell et al. 2000)
Carphodactylidae	*Nephrurus*	Bustard 1967
	Phyllurus	Mebs 1973 (in Marcellini 1977)
Diplodactylidae	*Lucasium*	Bustard 1965
	Rhacodactylus	Bauer et al. 1992
Eublepharidae	*Coleonyx*	Greenberg 1943
	Eublepharis	Marcellini 1977
Phyllodactylidae	*Gymnodactylus*	Evans 1936
	Ptyodactylus	Frankenberg 1974, 1975; Wever and Hepp-Reymond 1967; Werner 1972
	Tarentola	Henle 1839 (in Russell et al. 2000)
	Thecadactylus	Arturo Vale, unpubl. data
Sphaerodactylidae	*Euleptes*	Dolleschall 1855; Wiedersheim 1876 (in Russell et al. 2000)
	Sphaerodactylus	Regalado 2003
	Teratoscincus	Mebs 1996 (in Marcellini 1977)
Pygopodidae	*Delma*	Manley and Kraus 2010
	Lialis	Weber and Werner 1977
	Pygopus	Manley and Kraus 2010

with conspecifics (Marcellini 1974), in other species females vocalize during same-sex aggressive encounters (Jono and Inui 2012). Some species even have vocal repertoires of up to four different sounds (e.g., Tokay Geckos *Gekko gecko*; Brillet and Paillette 1991). Like birds and mammals, geckos appear to use vocal communication for territorial defense, sex recognition, and mating; thus, acoustic signals could play important roles in social interactions (Jono and Inui 2012).

Similarities between geckos and other distantly related vertebrates (e.g., birds, mammals, crocodilians) in the complexity and use of vocal communication could suggest that these complex social behaviours evolved early in vertebrates. Many of the tropical geckos associated with houses and urban areas vocalize (Table 1), providing excellent model systems. We studied the Northern Dtella, *Gehyra dubia* (Macleay 1877), a nocturnal and arboreal gekkonid lizard distributed throughout northeastern coastal Australia (Cogger 2014). This species is abundant on and around human dwellings, and is also common in nearby sclerophyll forests. Although this species produces at least three distinct call types (Tremul 2003), the full vocal repertoire of *G. dubia* is not well understood. We sought to clarify the vocal repertoire of this species, and determine whether the sexes differ in their use of vocalizations under different social circumstances.

MATERIALS AND METHODS

Study species.—Adult *Gehyra dubia* are solitary, but occasionally multiple individuals will use the same feeding or refuge sites. The mating season begins in late spring (September to November), and during summer (December to February) females produce several clutches of two eggs each (Wilson and Knowles 1988; Doughty 1996). Tremul (2003) described three calls in this species: (1) a single chirp sound; (2) a fast chatter (equivalent to the call we describe as a multiple single chirp); and (3) a distress call (equivalent to our multiple double chirp). Tremul (2003) observed a small number of both males and females making distress and single chirp calls, but apparently only males made the fast chatter.

Gecko collection and housing.—We collected geckos between August and November 2012 in the evening (1830–2030) around the James Cook University campus in Townsville, Queensland, Australia (19.3298°S, 146.7582°E). We located geckos by spotlighting on and around buildings and in surrounding sclerophyll forest. Geckos were captured by hand, occasionally encouraged to come within reach with a soft broom. We placed captured geckos into individual cloth bags, and took them to the laboratory where we determined the sex of each by everting the hemipenes, and measured snout-vent length (SVL, to the nearest 1 mm), tail-length (to the nearest 1 mm), and body mass (to the nearest 0.01 g). Based on the minimum size of gravid females in this population, we assumed that geckos with SVL > 45 mm were sexually mature. We used 40 adult males (mean SVL [±SE] = 57.9 ± 1.09 mm, range 46–69 mm) and 40 adult females (57.3 ± 1.23 mm, range 46–70 mm) in our study.

Geckos were housed in individual plastic cages (200 mm wide × 300 mm long × 100 mm tall) in a controlled-temperature room maintained at 25–26 °C with lights programmed to a 12:12 light:dark cycle. Each cage contained a shelter, paper-toweling substrate, and a drown-proof water dish containing fresh water. We monitored geckos daily, fed them crickets dusted with vitamin supplements twice weekly, and cleaned the cages once weekly. We released all geckos at their point of capture following our study.

Recording and classifying vocalizations.—We recorded gecko vocalizations under five social contexts: (1) males alone; (2) females alone; (3) male-male pairs; (4) female-female pairs; and (5) male-female pairs (n = 20 replicates of each treatment, total = 100 trials, each lasting 60 min). Individual geckos (n = 40 males and 40 females) were used a maximum of three times, once in each social context. We conducted trials between September and November 2012 at night (1900–2400) in a dark room maintained at 25–26 °C with a single low intensity light source positioned 0.5 m from recording arenas (desk reading lamp 240V 5W). For each trial, we transferred individual geckos from their home cages and placed them into a transparent plastic recording arena (230 mm wide × 340 mm long × 200 mm tall with a transparent lid containing air holes) either alone, or in pairs. We allowed geckos to acclimate for 30 min before the start of the trial. To distinguish individual geckos in the paired intrasexual and intersexual trials, we placed a small dab of colored, non-toxic nail polish (Be Yourself, GFA Australia Pty. Ltd., Victoria, Australia) on the dorsum of each gecko. Geckos shed their skin within one week of nail polish application, which completely removed the mark.

The lid of the recording arena contained a microphone (SONY F-V420, Uni Directional Dynamic Microphone, Frequency response 80–15,000 HZ, Sony Corporation, Tokyo, Japan) secured to the center. The microphone was connected to a sound recorder (Tascam DR–2d, Tascam, Tokyo, Japan or JamminPro HR–5 Linear PCM Recorder, Jammin Pro, New Jersey, USA), which together recorded all sounds made during the trials. To determine which individual was calling, we simultaneously recorded gecko behavior with a digital camcorder (Sony Handycam HDR-CX190E, Tokyo, Japan) placed 30 cm from the recording arena. Each trial lasted 60 min, after which time we transferred the geckos back to their home cages. After each trial, we washed all containers and lids thoroughly with hot, soapy water to remove any residual odor cues.

Data analysis.—We used Avisoft-SAS LabPro software (Avisoft, Berlin, Germany) to separate the recorded calls into different distinct vocalizations (call types) based on measurements of call length (s), call frequency (Hz), intervals within and between individual calls (s), the number of consecutive chirps, and obvious differences in spectrograms (Fig. 1). We did not analyze amplitude because our trials were conducted in small boxes, and amplitude likely would not have varied over these distances; geckos were never > 34 cm apart in our trials. We excluded from analysis very short calls produced by geckos when being bitten/charged by a conspecific (squeaks), as these only occurred during agonistic physical encounters (Tremul 2003). We used Avisoft-SAS LabPro software (Avisoft, Berlin, Germany) to separate the recorded calls into five distinct types (single chirp, double chirp, multiple single chirp, multiple double chirp, or triple chirp). We quantified the total numbers of each call type made by each individual gecko in each trial. We used these data to investigate sex-specific patterns of vocalizations by comparing the frequency of calls made by each sex among social pairing types. To do this we used a separate contingency table analysis for each call type. These analyses focus on understanding how sex (male, female) and social pairing (alone, same sex pairing, opposite sex pairing) influence the type and number of calls made. These analyses test the null hypothesis that males and females had similar calling rates when alone or in the presence of a conspecific of either sex.

Body size and sex of an individual can influence calling rate (Bertram 2000). To determine whether body size and sex influence calling rate, we used ANCOVA with SVL as the covariate and the number of single chirp calls produced as the dependent variable. To further examine the social context of vocalizations, we used linear regressions to examine the relationship between the number of calls produced by one gecko in each pair and the number of calls made by the other individual. This tested whether the calling rate of one individual

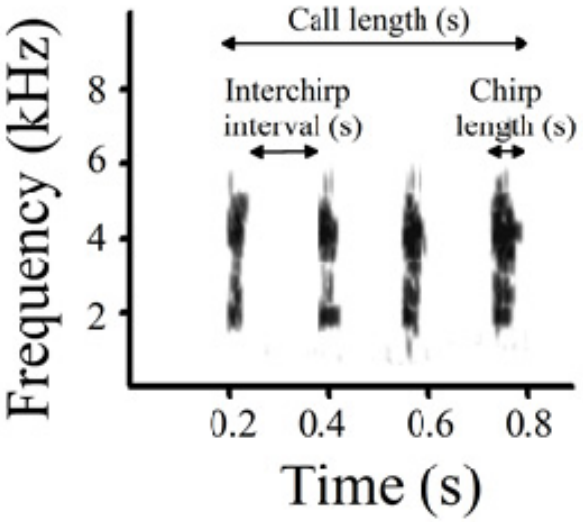

FIGURE 1. Schematic representation of how we quantified the frequency and duration of gecko vocalizations, using a multiple double chirp call as an example.

TABLE 2. Summary of the different types of vocalizations made by *Gehyra dubia* and their characteristics, shown separately for males and females. The frequency and duration of vocalizations are presented as average values, followed by the range in parentheses. We did not record any females making the multiple single chirp call.

Call type	Sex	Chirp(s) (#)	Low Frequency (Hz)	High Frequency (Hz)	Frequency Range (Hz)	Dominant Frequency (Hz)	Call Length (s)
Single Chirp	M	1	467.48 (10–1,227)	8,816.24 (6,829–11,471)	8,348.67 (6368–10639)	1,725.91 (188–5,063)	0.03 (0.023–0.063)
	F	1	442.85 (10–1,228)	8,791.35 (7,059–11,886)	8,348.94 (6389–11221)	2,311.79 (86–5,426)	0.03 (0.019–0.078)
Double Chirp	M	2	609.89 (77–1,381)	9,014.33 (7,366–11,138)	8,406.44 (6,752–10,723)	2,671.33 (188–4688)	0.09 (0.082–0.113)
	F	2	456.32 (77–921)	8,868.24 (7,059–10,281)	8,412.16 (6,829–10,051)	2,981.41 (188–4,737)	0.09 (0.05–0.123)
Multiple Single Chirp	M	14 (6–22)	432.64 (192–767)	10,861.43 (7,136–14,220)	10,428.79 (6,368–13,708)	3,674.57 (1,981–4,910)	2.31 (0.916–3.919)
	F	–	–	–	–	–	–
Multiple Double Chirp	M	3.7 (3–5)	588.22 (460–767)	9,931.67 (8,056–10,742)	9,343.56 (7,442–10,205)	3,604.67 (563–4,688)	2.57 (0.969–5.887)
	F	3.6 (3–6)	520.08 (230–691)	9,133.83 (6,714–10,742)	8,613.50 (6,074–10,128)	3,247.92 (563–4,910)	2.90 (1.4–5.993)
Triple Chirp	M	3	348.67 (86–587)	9,853 (8,224–12,205)	9,504.33 (7,682–11,865)	2,620.17 (188–3,938)	0.12 (0.095–0.138)
	F	3	533.667 (77–770)	9,483.93 (8,593–10,665)	8,961.87 (8,133–10,205)	2,894.40 (563–5,063)	0.11 (0.078–0.178)

depends upon the calling rate of the other individual, and thus whether they are communicating. We performed these analyses separately for each of the paired treatments (MM, FF, and MF) for each call type.

RESULTS

Call types and social context of vocalizations.—We recorded vocalizations from 100 *G. dubia* trials, split equally among solitary males, solitary females, male-male pairs, female-female pairs, and male-female pairs (n = 20 of each treatment). From 100 hours of audio recordings, we identified five distinct types of vocalizations produced by *G. dubia*, three of which have not been previously described in geckos (Table 2). Overall, the frequency and length of each call type was similar for both males and females (Table 2).

Single Chirp Calls are short, single sounds that may be repeated, but not as a continuous series of chirps at short and similar intervals (Supplementary Audio 1; Table 2; Fig. 2a). This was the most frequent call type and was used by almost all individuals, both when alone and when paired with a conspecific of the same or opposite sex (Figs. 3 and 4). Within the sexes, we found no significant differences in the proportion of individuals calling or not calling among the different treatments (alone, or paired with a conspecific; M vs MM vs MF; $\chi^2 = 0.78$, $df = 2$, $P = 0.67$; F vs FF vs MF; $\chi^2 = 1.87$, $df = 2$, $P = 0.39$; Figs. 3 and 4). Overall, females generally made more single chirps than males (Fig. 4).

Double Chirp Calls are short sounds comprised of two chirps that were connected on the sonogram, but did not occur as a continuous series (Supplementary Audio 2; Table 2; Fig. 2b). Although double chirp calls were produced by both males and females when alone and when paired with a conspecific, this call was significantly more likely to be used in the presence of a conspecific of the same or opposite sex than when alone, for both males (M vs MM vs MF; $\chi^2 = 15.62$, $df = 2$, $P < 0.01$) and females (F vs FF vs MF; $\chi^2 = 20.28$, $df = 2$, $P < 0.01$; Table 3; Figs. 3b and 4b). Overall, double chirps increased in the presence of a conspecific, and females used this call at twice the rate of males (Fig. 4b). This call usually occurred during and after displaying aggressive behaviors towards a conspecific, and was typically made by the individual instigating the aggressive behavior.

Multiple Single Chirp Calls are comprised of a series of chirps produced in a continuous series, equally spaced in time (Supplementary Audio 3; Table 2; Fig. 2c). The number of chirps in a multiple single chirp call ranged from 6–22 consecutive chirps per call, but this range varied substantially among individuals. Male geckos used this call only rarely, and we did not record any females producing it (Figs. 3c and 4c). Multiple single chirp calls occurred when male geckos were alone, and when they were paired with a conspecific; males doubled the rate of multiple single chirp calls in the presence of females, although this was not significant (M vs MM vs MF; $\chi^2 = 4.69$, $df = 2$, $P = 0.09$; Fig. 4c).

Multiple Double Chirp Calls consisted of a continuous series of double chirps, spaced at roughly equal time intervals (Supplementary Audio 4; Table 2; Fig. 2d).

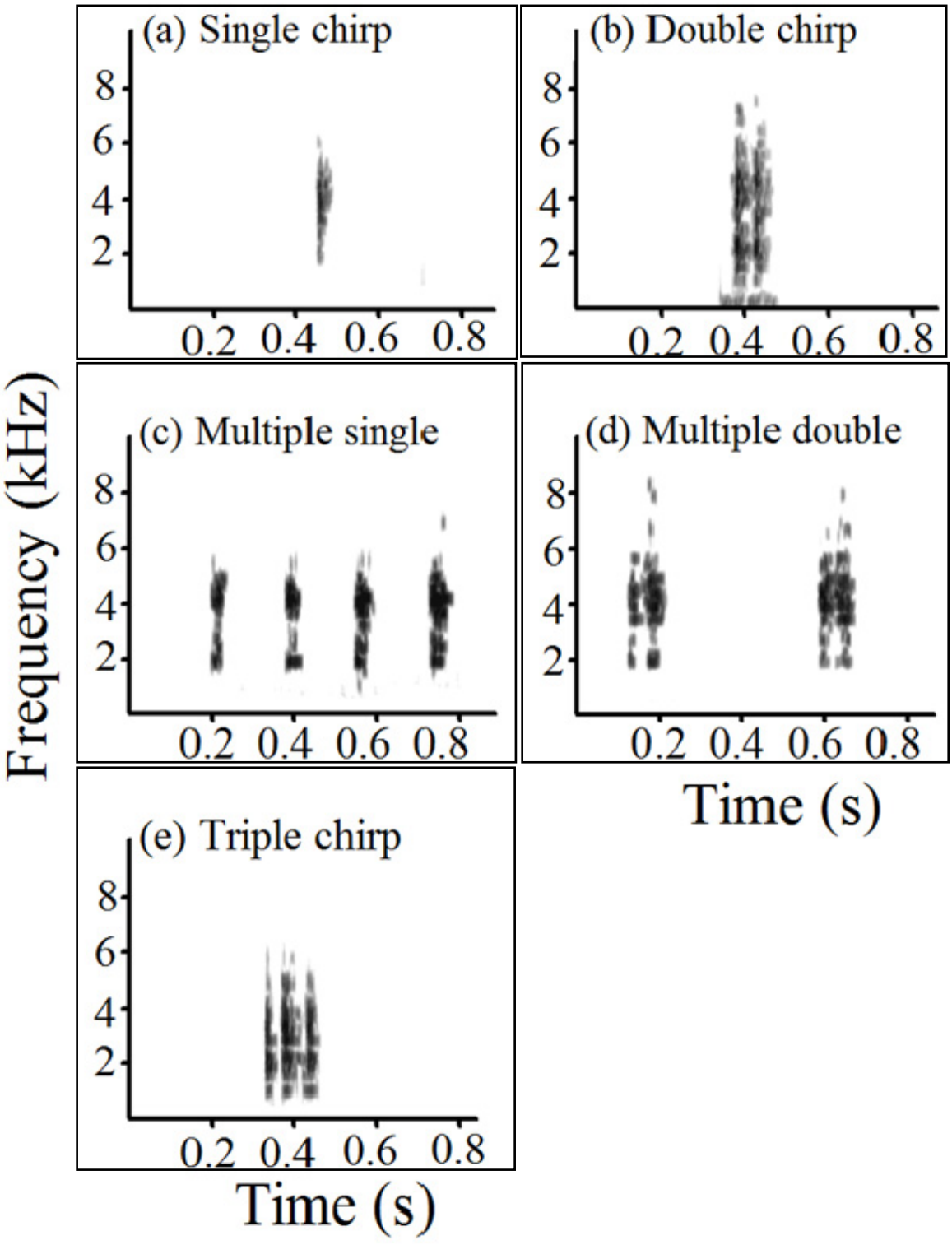

FIGURE 2. Representative spectrograms of the five call types recorded from *Gehyra dubia*: (a) Single chirp, (b) Double chirp, (c) Multiple Single Chirp, (d) Multiple double chirp, and (e) Triple chirp. Summary statistics for these call types are provided in Table 2, and examples of each call are provided in the Supplementary Audio files. Calls are also embedded in this PDF. Click on the respective graph above to hear that call. (If no sound is heard, check your speaker and pdf settings, and that you have the most recent version of Adobe Reader™).

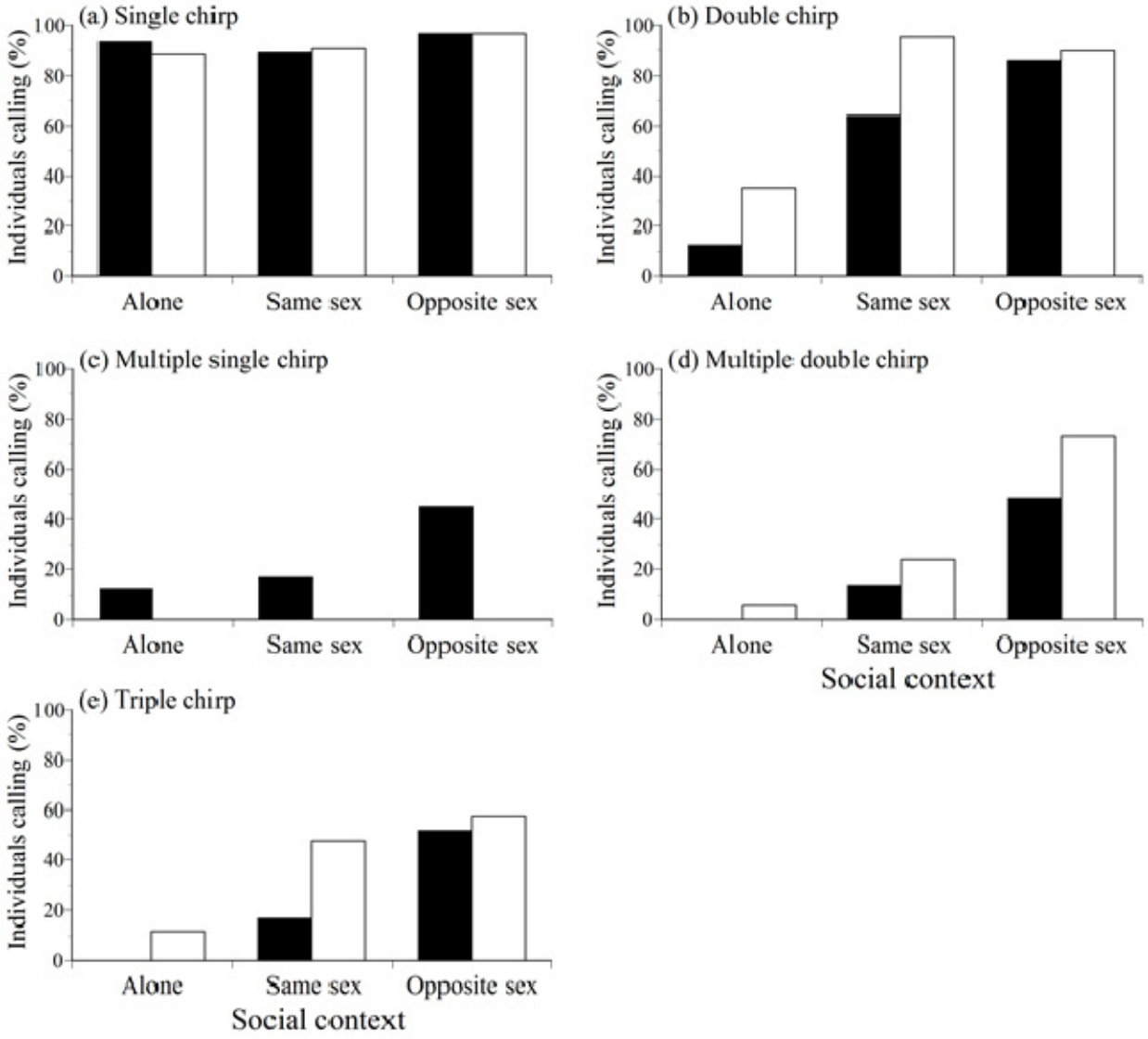

FIGURE 3. Calling frequencies of male (black bars) and female (open bars) *Gehyra dubia*, expressed as the percentage of individual males and females tested that made each call type: (a) Single chirp, (b) Double chirp, (c) Multiple Single Chirp, (d) Multiple double chirp, and (e) Triple chirp. We did not record any instances of female geckos producing the multiple double chirp.

The numbers of consecutive double chirps in each call varied among individuals, ranging from three to six double chirps per call, with no particular pattern associated with individual geckos. This call was produced by both male and female geckos, but was rarely produced when alone, and was significantly more likely to occur when geckos were paired, especially in the presence of a conspecific of the opposite sex (M vs MM vs MF; $\chi^2 = 11.47$, $df = 2$, $P < 0.01$; F vs FF vs MF; $\chi^2 = 16.40$, $df = 2$, $P < 0.01$; Fig. 3d). Sometimes aggressive behavior also occurred before the attacking gecko produced this call, including chasing, attempted biting, and successful biting. Male and female geckos used multiple chirp calls, especially during aggressive encounters with a conspecific, but females used this call more often than males (Figs. 3 and 4). Sometimes the attacking gecko displayed aggressive behavior before producing this call, including when chasing or biting another individual.

Triple Chirp Calls consisted of three chirps in a row, with equal time intervals between each chirp (Supplementary Audio 5; Table 2; Fig. 2e). Both male and female geckos produced triple chirps, but females generally produced this call more often than males, either when alone or paired with a conspecific (F vs FF vs MF; $\chi^2 = 10.35$, $df = 2$, $P < 0.01$; Fig. 3e and 4e). Males rarely produced this call when alone, but sometimes produced it in the presence of female (M vs

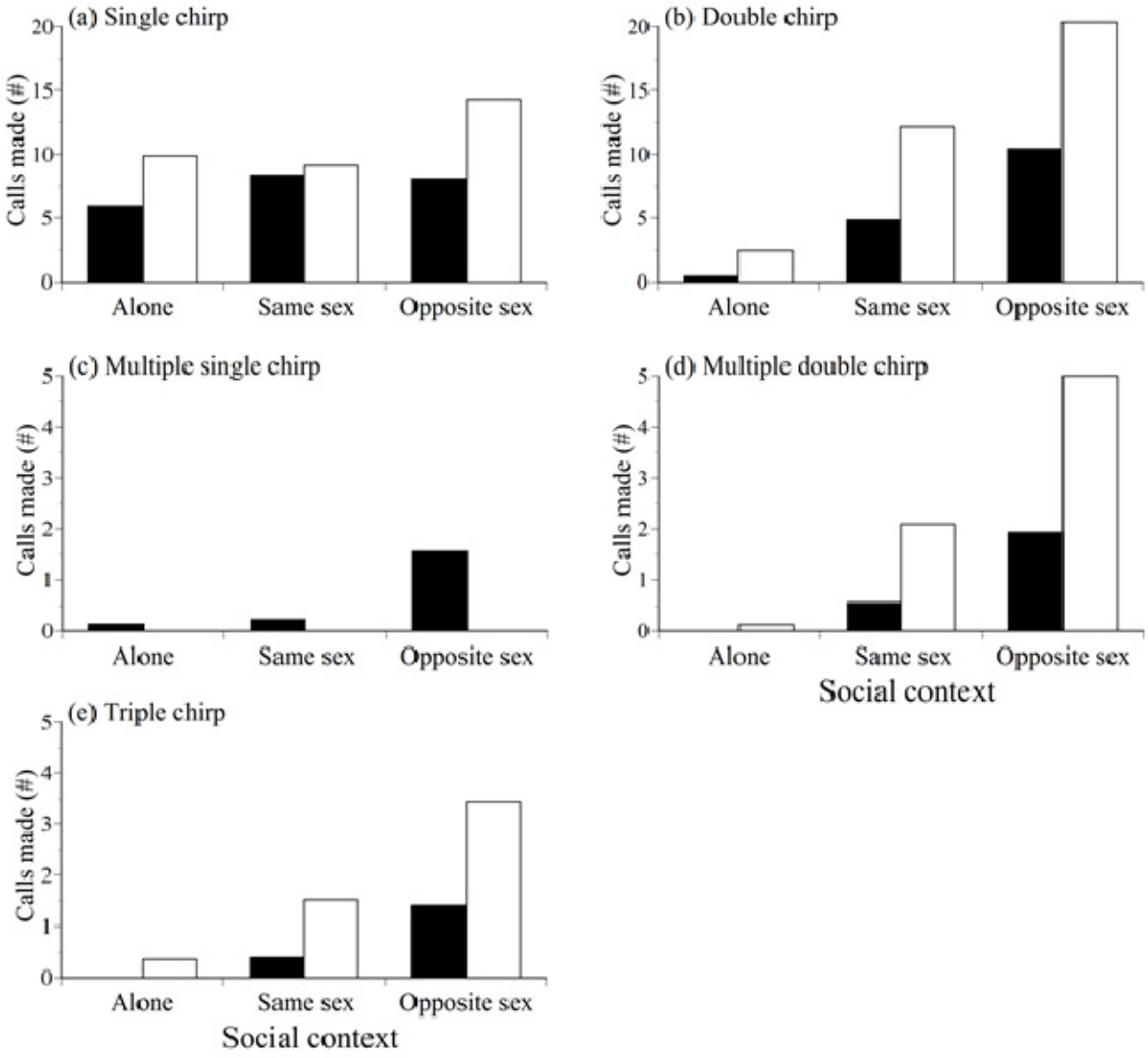

FIGURE 4. Calling rate of male and female *Gehyra dubia*, expressed as the mean number of calls per hour, shown separately for males (black bars) and females (open bars) by call type: (a) Single chirp, (b) Double chirp, (c) Multiple Single Chirp, (d) Multiple double chirp, and (e) Triple chirp. We did not record any instances of female geckos producing the multiple double chirp.

MM vs MF; χ^2 = 7.59, *df* = 2, $P < 0.01$; Fig. 3e). Overall, geckos increased calling rate in the presence of a conspecific, especially a member of the opposite sex (Table 3).

Body size context of vocalizations.—Body size (SVL) and sex significantly influenced calling rate of geckos for single chirp calls (Sex: $F_{1,105} = 6.80$, $P = 0.010$; SVL: $F_{1,105} = 18.60$, $P < 0.001$; Fig. 5). Larger individuals used single chirp calls significantly more often overall than smaller individuals, and females vocalized significantly more than males at all body sizes (Fig. 5). For all other call types (which are used much less frequently; e.g., Figs. 3 and 4), there was no significant relationship between body size and calling rate (all $P > 0.05$).

We found strong evidence that both individuals in a pair exchange auditory information during social encounters, because the calling rate of both geckos in a pair were strongly, positively related for multiple double chirps during female-female trials ($r^2 = 0.69$, $F_{1,9} = 20.17$, $P = 0.002$; Fig. 6), for single chirps and triple chirp calls during male-male trials (all $r^2 > 0.38$, $F_{1,9} > 5.45$ $P = 0.040$; Fig. 6), and for all call types during male-female trials (except for multiple single chirps, which females do not make; all $r^2 > 0.27$, $F_{1,9} > 5.08$, $P = 0.040$; Fig. 6). These patterns were not caused by body size differences between paired geckos, which did

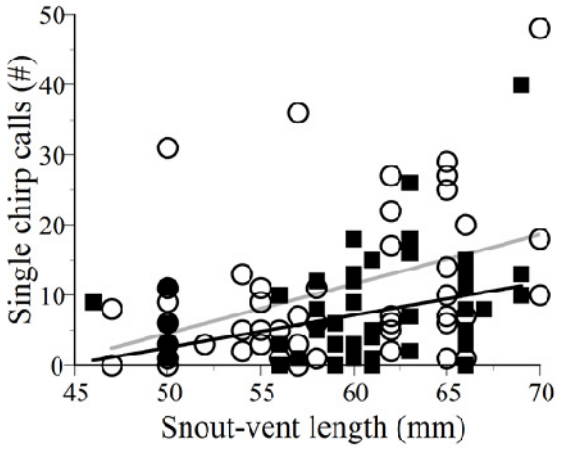

FIGURE 5. Relationship between *Gehyra dubia* body size (SVL) and calling frequency (the number calls made during a 60 min trial) of single chirps, shown separately for males (squares, black line) and females (open circles, grey line). Larger geckos tend to call more frequently, but females at all body sizes call more often than males.

not significantly influence calling rate (for all call types, all $P > 0.05$), likely because all animals we used were adults (body size differences between paired geckos ranged from 0–8 mm SVL).

DISCUSSION

We found that the native Australian Northern Dtella produces calls in a frequency range approaching the limits of human hearing, from 6,000 to 13,000 Hz. Both male and female geckos vocalize when alone, as well as in pairs, indicating that some vocalizations were broadcast signals, but others were likely used for inter-individual communication. The call repertoire of *G. dubia* includes at least five distinct vocalizations: single chirps, double chirps, multiple single chirps, multiple double chirps, and triple chirps. Although males were the only sex to make multiple single chirps, females were more vocal overall in terms of the propensity to call, and the numbers of calls made. Both male and female *G. dubia* produced calls similar in frequency, structure, and duration. We observed several aggressive responses directed towards conspecifics during intra and intersexual encounters, and these were often accompanied by vocalizations. Overall, this strongly suggests that vocal communication is important during a wide range of social interactions in this species, and that females are generally more vocal than males.

During handling, some *G. dubia* produced single chirp calls. Other gecko species also produce a single chirp call during conspecific aggressive encounters; including both Asian House Geckos, *Hemidactylus frenatus* (Marcellini 1974), and Mediterranean House Geckos, *H. turcicus* (Frankenberg 1982). Single chirp calls are common among gecko species that vocalize, and may be used to broadcast information. Because geckos sometimes produce calls during handling, some researchers have concluded that these calls serve as distress signals (e.g., in *H. frenatus*; Marcellini 1974, 1977), but this warrants further testing.

The double chirp call was produced by both male and female *Gehyra dubia*, and was more likely to be made during conspecific encounters, especially by females. Double chirp calls were often made by the aggressor in conjunction with aggressive acts (e.g., chasing, fighting, biting, etc.), perhaps to assert dominance. Double chirp calls have not yet been reported in any other gecko species.

Multiple single chirp calls (the "fast chatter" reported by Tremul 2003) were produced by male *Gehyra dubia*. In contrast, both sexes of other gecko species produce this call, including *H. frenatus* (Marcellini 1974) and *G. japonicus* (Jono and Inui 2012). Multiple single chirp calls are known from many gecko species, including *H. frenatus*, *H. mabouia*, *Ptenopus garrulus*, and *G. japonicus* (Marcellini 1974; Regalado 2003; Hibbitts et al. 2007; Jono and Inui 2012). In *H. frenatus*, multiple chirp calls are used after eating or mating, during courtship and copulation, and during aggressive encounters (Marcellini 1974). Male Barking Geckos (*Ptenopus garrulus)* use multiple single chirp calls to advertise their body size and attract females to their burrow (Hibbitts et al. 2007). It is possible that male *G. dubia* also use multiple single chirps to attract females, but we did not observe mating behaviors during our study. Clearly, experiments examining gecko behavior in more natural settings are required to clarify which social interactions elicit this call in *G. dubia*. In our experiments, multiple double chirp calls occurred during aggressive encounters between same- and opposite-sex individuals, likely sending a signal of aggressive intentions.

In our experiments, multiple double chirp calls occurred during aggressive encounters between same- and opposite-sex individuals. Multiple double chirps were likely used as a signal of aggressive intentions in this species, and have not been recorded in other gecko species. Finally, triple chirp calls often occur during conspecific encounters, and are mostly emitted by females. However, these calls are uncommon, and there appeared to be no clear association between this call type and specific behaviors, so the function of this call is not well understood. Triple chirp calls have not been recorded in other gecko species.

Even though our trials were conducted at a time when mating and breeding was expected, we did not observe these behaviors during our experiment. This was likely because, in our experimental design, males and females were only paired for one hour. Nonetheless, understanding whether there are additional call types associated with these behaviors, or whether calling

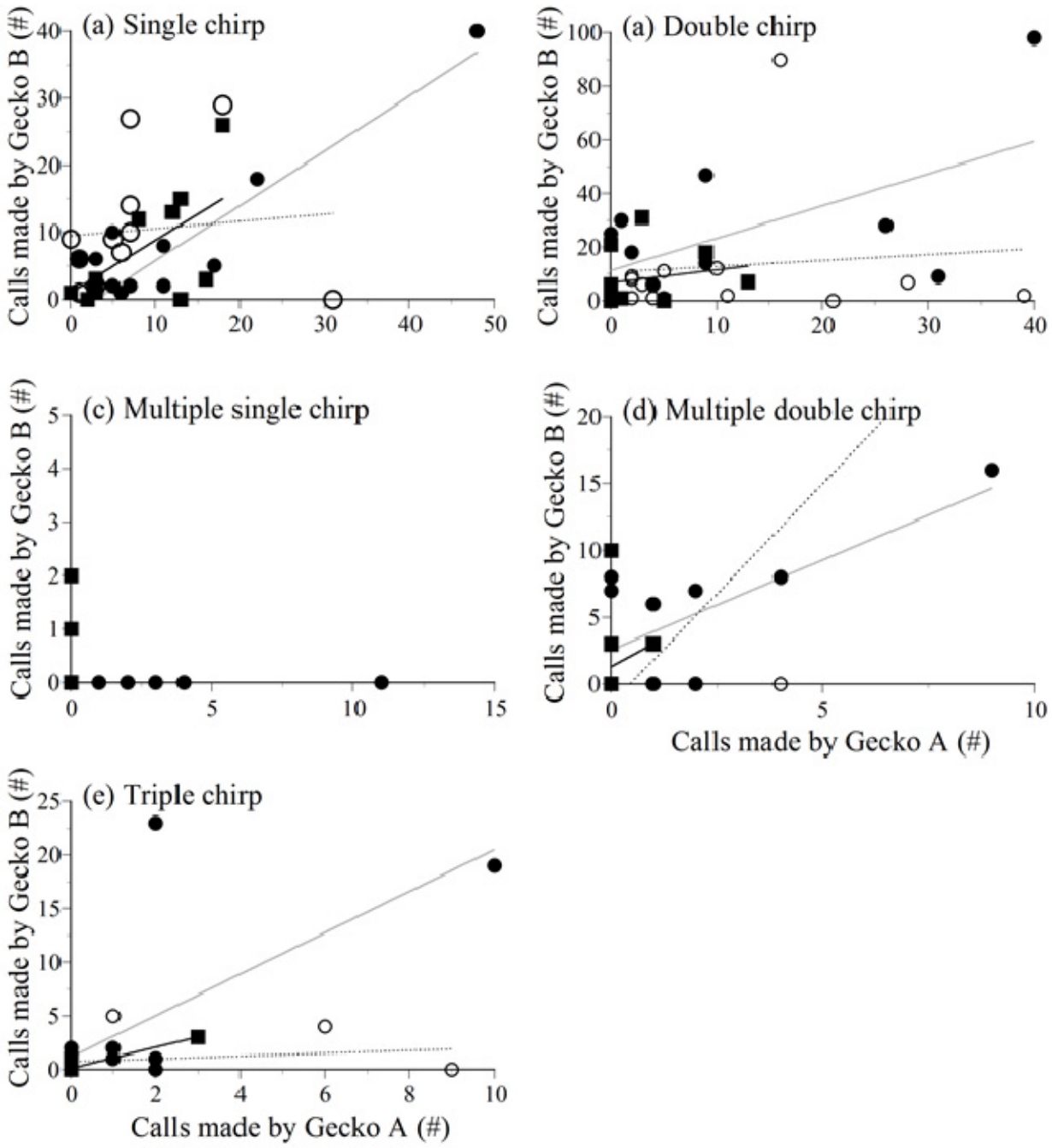

FIGURE 6. Relationships between numbers of calls made by one individual *Gehyra dubia* and the other individual in paired treatments (shown separately for male-male [closed squares, black line], female-female [closed circles, gray line], and male-female pairs [open circles, dotted line]), shown separately for each call type: (a) Single chirp, (b) Double chirp, (c) Multiple Single Chirp, (d) Multiple double chirp, and (e) Triple chirp. In the male-female trials, gecko A is the male and gecko B is the female.

behavior changes during mating will more fully elucidate the functions of these calls. Moreover, there may be additional calling behaviors that occur during different parts of the life cycle, due to ontogenetic or seasonal changes that we did not observe. Further study of these topics will improve our knowledge and understanding of vocal communication in gekkonid lizards.

Human ears can detect sounds ranging in frequency from 20 to 20,000 Hz (Cutnell and Kenneth 1998), and most studies of vocal communication in animals focus on species that produce loud or low frequency calls within this range. In gekkonid lizards, most vocal communication studies focus on species with relatively

loud and conspicuous calls (e.g., *H. frenatus*, *G. gecko*, and *Ptenopus* sp.; Marcellini 1974; Tang et al. 2001; Hibbitts et al. 2007). For example, the globally invasive *H. frenatus* vocalizes within the frequency range audible to human hearing (1,500 to 2,500 Hz), and can be heard over long distances of up to 150 m (Marcellini 1974). The hearing limits and vocalization energy of some pygopod geckos extend to frequencies far above 20 kHz (Manly and Kraus 2010). By contrast, *G. dubia* produces vocalizations relatively cryptic to the human ear, and are thus much less conspicuous.

Gehyra dubia calls can be separated easily into five distinct call types, which is more than has been described in the literature for other squamate reptiles. For example, *H. frenatus* uses only three call types (single chirps, multiple chirps, and a 'churr' call) in their communication (Marcellini 1974). Two of the call types produced by *G. dubia* (single chirps and multiple chirps) are common to many gecko species around the world, including both sexes of *H. frenatus*, *H. turcicus*, *G. japonicus*, and *Ptyodactylus* sp. (Marcellini 1974; Frankenberg 1974, 1982; Jono and Inui 2012); however, three of these calls (double chirps, multiple double chirps, and triple chirps) are, as far as we can ascertain, unique to this species. Identifying the social context within which calls are made, and the selective forces resulting in differences in sound production among taxa, are necessary to determine the functional significance of vocalizations in squamate reptiles.

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SUPPLEMENTARY AUDIO FILES

We reduced external noise and amplified the original recordings so that the calls are clearer and more audible to the human ear.
Audio 1: Example of a single chirp call (http://www.herpconbio.org/Volume_9/Issue_2/aud1.wav)
Audio 2: Example of a double chirp call (http://www.herpconbio.org/Volume_9/Issue_2/aud2.wav)
Audio 3: Example of a multiple single chirp call (http://www.herpconbio.org/Volume_9/Issue_2/aud3.wav)
Audio 4: Example of a multiple double chirp call (http://www.herpconbio.org/Volume_9/Issue_2/aud4.wav)
Audio 5: Example of a triple chirp call (http://www.herpconbio.org/Volume_9/Issue_2/aud5.wav)

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